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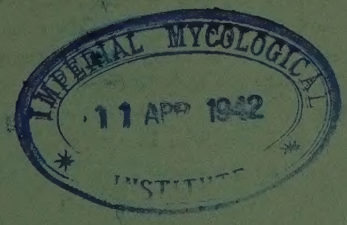
CONTENTS

Some Views of the Morphology and Phylogeny of the Leafy Vascular Sporophyte ... ISABEL M. P. BROWN 383

Contemporary Understanding of Bacterial Plant-Diseases and their Causal Organisms ..... C. STAPP 405



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THE BOTANICAL REVIEW

VOL. I OCTOBER, 1935 NO. 10

SOME VIEWS ON THE MORPHOLOGY AND PHYLOGENY OF THE LEAFY VASCULAR SPOROPHYTE

ISABEL M. P. BROWN
Surrey, England

AT THE PARTING OF THE WAYS

Dr. Scott, in the last edition of his "Studies in Fossil Botany," remarked that recognition of the Psilophytales had led us to look at the whole question of relationships among the higher classes of plants from a new point of view (53, *387*). In the twelve years that have passed since these words were written, a number of fresh and curious types, either belonging to or suggesting affinity with the Psilophytales, have been described. While the problem of the interrelationships of the Pteridophyta has been perhaps complicated rather than solved by these discoveries, the importance for phylogeny of the Psilophytales, the predominantly Devonian phylum, has certainly been increased.

Is this phylum to be regarded as a primitive group of vascular cryptogams? Nearly all botanists seem to hold that even if the Psilophytales known to us are not the direct ancestors of geologically less ancient phyla, the group as a whole and, in particular, its best known family, the Rhyniaceae,[1] are of highly primitive construction and thereby give us the clue to the other pteridophytic phyla (*27, 775;* 28, *617;* 30, *842;* 5, *5–6;* 7, *122;* 54; 53, *420;* 55, *155;* 57; 22, *176, 692;* 63, *108;* 10, *494–501;* 33). Church, however, does not regard the Rhyniaceae as Pteridophyta but as primitive Bryophyta in process of reduction from more freely branched algal forms. The theory of the origin of the Bryophyta by reduction does not concern us here, but the recognition that the plant-body of the Rhyniaceae, as known to us, is a vascular sporophyte,

[1] In the present article, this family is held to include *Rhynia, Hornea* and *Asteroxylon.*

such as is found among cryptogams only in the Pteridophyta (27, *779*) is of fundamental importance. Even if it be not possible, as Church declares, to prove lignification of the tracheid-like cells in *Hornea,* owing to chemical changes during fossilization, it would still hardly be possible to interpret them, as Church does, as of the nature of the ringed unlignified cells found in some recent Bryophyta, in the face of certain sections (28, *pl. VIII, f. 47* and *pl. VIII, f. 48*). And *Hornea* does not stand alone; its anatomical similarity to *Rhynia major* makes it clear that both plants are constructed on the same anatomical plan. *Rhynia major* has a relatively well developed and preserved vascular cylinder. Church believes that the land was colonized by maritime algae in a single transmigration by the raising of the floor of the ocean, the rocks thus raised carrying with them all the plants growing on them, but that only the most highly organized of them—more highly organized than any *single* algal form at present known to exist in the sea—became the ancestors of the Pteridophyta. He holds that it "admits of no reasonable doubt" that these algal ancestors of the Pteridophyta were fine plants, three to six feet long. He also asserts that on leaving the sea they already possessed morphologically differentiated main axes, lateral and dichotomous ramification, root ("crampon") ramuli, definitely delimited "bilateral" ramuli (*i. e.,* leaves), Fibonacci symmetry, and "even axillary habit in the laterals" (11, *88–90*). Later he lays down the general law that the initial stages of leaf-production are solely a phenomenon of the sea (12, *134*).

It may well be that the primitiveness of the Rhyniaceae has sometimes been overstated. Kräusel, for instance, argues that in the Psilophytales we have true vascular plants, but of an organization so simple that no simpler one could be imagined (33, *7–8*). Scott has suggested, on the other hand, that the Rhyniaceae, though primitive in general organization, may have undergone some reduction, as their peaty habitat suggests (53, *391*). But that they are primitive seems to be shown by the structure of their sporangia. In *Hornea* the sporangium evidently arose by transformation of the tips of certain branches, and when one of these was in a condition of incipient branching the sporangium, with its columella, partook of this dichotomy. In *Rhynia Gwynne-Vaughani* Kidston and Lang found two unusual sporangia in which spores were

apparently formed at the end of a branch (28, *607*); the word used is "stem," but branch seems a more suitable term) "without its being actually modified into a sporangium." The same writers draw attention to the fact that as early as 1908 Schenck had shown that the algal structures strictly corresponding to the pteridophytic tetrad of spores and the spore-mother-cells were respectively the algal tetraspores and tetrasporangia in which meiosis takes place (30, *851*). Even if, as they suggest, we are here dealing with a homoplastic similarity which is an expression of general morphology rather than of relationship (28, *622*), we can hardly fail to recognize in it an argument in favor of the primitiveness of the morphology of the Rhyniaceae and of their origin from a group with spore-producing organs of an algal type. Moreover, for the same reason and because of poorness of the geological record of the Anthocerotes, it is difficult to accept Campbell's view that the Rhyniaceae and the earliest vascular cryptogams were, if not actually Anthocerotes, at any rate probably much like them (9, *74*; 10, *492*). It may be noted here that Zimmermann's exposition of Campbell's views is misleading (63, *88*); the views given as Campbell's are much nearer to, though not identical with, those of Church, and may have arisen by a confusion of these two conflicting points of view.

If the Rhyniaceae are reduced, there is every reason to believe that they are reduced from primitive leafless forms. Of recent years a number of leafless members of the Psilophytales have been described, as *Hicklingia* (31, 36) and *Taeniocrada,* under which Kräusel and Weyland include five species, the best known being *T.* (*Haliserites*) *Decheniana* Goepp. (37, 39). Only two will be shortly described here. *Gosslingia breconensis* Heard (20) was older, larger, and possessed a much better developed (exarch) protostele than *Rhynia* and bore its sporangia on a special short branch, variously interpreted and even compared to an axillary branch. *Pseudosporochnus Krejci* Pot. & Bernard was a large plant, reaching a height of over six feet.[2] It had a main axis up to 5 cm. in diameter, giving rise by repeated dichotomies to a crown of main branches. These themselves forked once or twice and gave off laterally a number of much shorter and more slender dichotomous branches, the ultimate branches bearing terminally

[2] The latest researches seem to show that estimates turning this plant into a small tree over nine feet high are based on remains that can not be safely identified as *Pseudosporochnus* (40).

narrow wedge-shaped sporangia which were themselves sometimes forked, presumably a primitive character. Neither of these plants can be regarded as reduced and yet they, too, are quite leafless. Zimmerman believes that not all the wedge-shaped expansions were sporangia and that some of them may be regarded as the first indications of laminar development (63, *111–112*).

Moreover, Church's views involve, as Bower has pointed out, the tremendous assumption that in nature the colonization of the land by marine organisms occurred but once (6, *243*). Bower also refers to Church's theory as one in which it is assumed that organic nature could not, or probably would not, originate new members in more than one phyletic line. Church, however, takes an extreme polyphyletic view of the origin of the land flora and regards not only the pteridophytic phyla but the flowering plants as lines that probably reached back independently to the sea (11).

It has come to be widely accepted that from dichotomous thalloid vascular sporophytes two main forms of leaf-bearing plants have been evolved, the small-leaved and the large-leaved. It is believed that primitively large leaves represent thalloid branch systems that have become flattened and appendicular with reference to a relatively main axis, but that primitively small leaves represent either emergences from a preëxisting axis or ultimate branchlets of a thallus. Goebel, however, saw no reason to doubt the homology of the leaf in ferns and lycopods, the typically megaphyllous and typically microphyllous groups. He held that the attempt to homologize the lycopod leaves with the paleaceous scales (he does not mention the Aphlebiae by name in this connection) of the frond and the frond itself with a flattened branch-system came to grief over the clear agreement between these scales and the hairs which in some ferns occupy their place. To look upon the hairs as reduced paleae would, he said, place too great a strain on a hypothetical construction already poorly equipped (15, *914*). Those who support the emergence theory of the lycopod leaf would be more likely to derive the palea from the hair than *vice versa*. I have not been able to obtain a sight of the third edition of Goebel's book to see if he had changed his views.

THE EARLY MICROPHYLLOUS FORMS

The Lycopodiales are typically microphyllous and a number of botanists believe that their leaves originated, phylogenetically speak-

ing, as emergences or outgrowths from a preëxisting axis. This view, formulated by Lignier (47, 48), has, in varying forms, received support from Halle (19, *36*), Arber (2, *73*), Hirmer (22, *691*), Kräusel (33), Seward (61), Bower (*7, 552*), and other botanists.

More than twenty-five years ago Tansley pointed out that, while the possibility that the lycopod leaf owed its simplicity to reduction during phylogeny could not be excluded, yet, if the said leaf were held to be derived by foliar specialization of the short undivided branchlets of the thallus rather than of whole branch-systems, as in the ferns, it was possible "to bring the lycopods into line with the other Pteridophyta without either hypothecating extreme reduction or abandoning an explanation of the morphological nature of the leaf which seems by far the most rational and convincing that has ever been suggested" (62, *5, 9*). And in 1921 Kidston and Lang were inclined to think that, on the whole, the organization of *Rhynia, Hornea* and *Asteroxylon* weighed against too sharp a distinction between large and small leaves and in support of Tansley's last mentioned view (30, *848*). Lang, however, has since come to entertain the possibility that the simple leaves of some typical lycopods may prove to have arisen as emergences (44, *437*).

Zimmermann accepts the origin of fern fronds from branch systems. His views on the origin of small leaves are difficult to summarize. He holds that in primitive vascular thalloid plants the plant-body was made up of units which he calls *telomes*. Each telome represents a single branchlet or segment, in so far as such are single and unbranched ("einachsig"), according to the course of the vascular strand as well as in the form of the branchlet. Each telome starts, theoretically speaking, at its junction with another telome and ends (except, of course, in the case of terminal telomes) at the starting point of the next telome. Fertile telomes are represented by the sporangium, apparently with its vascular stalk (63, *65, f. 22*); each sterile telome he calls a *phylloid*, using this word in a different sense from that of Lignier, who first used it for small leaves that are believed to have arisen as emergences. The telomes, fertile and sterile, are regarded as homologous and equivalent (63, *65*).[3] To Zimmermann, large and small vegetative

[3] I can see no justification for Bower's statement that Zimmermann reduces the whole wealth of form characteristic of living Cormophyta to a fundamental organ, the telome, consisting of distal sporangium and a stalk, usually

leaves are combinations of sterile telomes, differing in the number of telomes that have, so to speak, been used up in the formation of the leaf. Though he speaks of each of his single "phylloids" as becoming directly converted by means of a greater or less amount of flattening and laminar development ("flächenförmige Verbreiterung") into a simple uninerved leaf, such as is found today in *Lycopodium* and *Equisetum,* this appears to be a description, in terms of telomes, of an ontogenetic process occurring today. In the same paragraph he adds "Often, *e.g.,* in the Lycopsida and Articulatae, there was at first in the position of a simple phylloid a complex of phylloids (Phylloidstand)" and urges that this indicates that the simple or "lyco-leaf" was in its earliest morphology equivalent to a freely branched branch-system of phylloids developing as a shoot (63, *65–67*). On the following page he remarks that in its ontogeny and before branching sets in, every complex of telomes ("Telomstand") is a telome. And in discussing *Protolepidodendron Scharyanum* he says that this oldest of the Lycopsida still shows us, as a vestige from its ancestors, the forking leaves, represented in all divisions of the Pteridophyta, but which do not occur later in the Lycopdiales (63, *130*).

It is possible to look upon the hemispherical protuberances on the axis of *Rhynia Gwynne-Vaughani* as rudimentary emergences comparable to but more primitive than the spines of *Psilophyton.*[4] *Dutoitia pulchra* from the Devonian of South Africa might seem to support the idea of rudimentary emergences, since its dichotomous axes, terminating in relatively large and obconical organs, are highly reminiscent of *Rhynia* and some of them bear appendages "in the shape of hemispherical protuberances or spines which may attain a length of 1 mm." (*23, 92, f. 1*). Unfortunately, however, the vascular nature of *Dutoitia* is not established. Kidston and Lang, who first described the protuberances of *Rhynia Gwynne-Vaughani,* came to the conclusion that they did not represent an early step in the origin of small leaves, partly because they

with vascular supply; nor for the further statement that in Zimmermann's view microphylls and megaphylls alike represent sterilized telomes (*6, 617*). The latter author regards fertile and sterile telomes (which, he points out, occur both separate and mixed in telome complexes, his "Telomstände") as originally homologous and equivalent. This seems a natural view for one who, like Bower (cf. *6, 490, 615–617*), is inclined to look upon the vascular sporophyte as a generation homologous with the gametophyte (*63, 86–88*).

[4] Arber held that the two structures were equivalent (*2, 24–25*), but later researches have shown that they were markedly different.

originated late in the ontogeny and were frequently formed underneath a stoma. There seems, however, to be no particular reason why an emergence, ultimately serving a photosynthetic purpose, should not originate beneath or close to a stoma. Nor would the fact that these protuberances "cannot be regarded as part of the primary construction of the plant as at first developed" (30, *833*) militate against the view that they are homologous with, or at any rate forerunners of, the spines of *Psilophyton* and the small leaf of *Lycopodium;* since these structures would, *ex hypothesi,* be phylogenetically new parts, arising from a preëxisting axis and not in the same morphological category as a primary part of the plant body. Lang's recent work on the spines of *Psilophyton princeps* has strengthened the view that these structures were morphologically emergences, probably of a glandular nature. Not only are they irregularly arranged and variable in size (from under 0.5 to over 2 mm. in length), but large and small spines are often inserted close together. Lang found no traces of vascular tissue in numerous and well preserved spines from Canada and Scotland (44, 43), so that there is a strong presumption that they were devoid of vascular tissue. Two fossils, probably belonging to the Psilophytales, seem to have had emergences even less leaf-like than the spines of *Ps. princeps.* In *Ps. wyomingense* Dorf from the early Devonian, the irregularly arranged spines were less dilated at the base, finer and closer together (14, *242*). In this species the tips of the branches were not circinate, giving the plant a more Lycopodium-like appearance; the sporangia are unknown. In *Dawsonites Ellenae* from the Mid-Devonian of Norway both fertile and sterile axes bear a few spines which are usually very small, though they range from 0.5 to just over 1 mm. in length (25, *4, f. 1* and *pl. II, f.* 5). In this species the sporangia seem to be rather wider than long and are borne in clusters, much as in *Taeniocrada decheniana* (37, *38*). On the other hand, vascular elements have been found in the spines of *Arthrostigma gracile,* a contemporary species so like *Ps. princeps* that only recently has it been shown that they were not parts of the same plant (21, 43). And in *Drepanophycus spinaeformis* from the Mid-Devonian rocks, another very similar form, the spine-like "leaves" show a midrib which was presumably vascular.[5]

[5] Kräusel and Weyland consider that this and *A. gracile* are certainly generically identical and may be conspecific, and on grounds of priority they would call the latter *Drepanophycus gracilis* (37).

From such appendages to the more leaf-like emergences of the Lower Devonian and Mid-Devonian genus *Asteroxylon* seems but a short step. For in this genus, besides the upper fertile naked branches of the *Hostimella*-type, there are regions of the axis which bear spines and are indistinguishable, when found detached, from *Psilophyton*. In this condition they are originally described as *Psilophyton princeps* (34, *182, pl. VIII, f. 14; pl. IX, f. 20*). These spiny regions are in turn succeeded, toward the bases of the axes, by regions in which the spines pass gradually into densely set scale-leaves (35, *120*). There is no evidence of vascular tissue in the spines or scale-leaves of either of the two known species of *Asteroxylon, A. elberfeldense* or *A. Mackiei,* though in the latter traces run from the axial cylinder to the base of the leaf (29). It seems significant that Seward should have established the genus *Haplostigma* for stems which appear, in the absence of petrified material, to be in some ways intermediate between Psilophytales from the Lower and Middle Devonian and more highly specialized arborescent lycopods from the Upper Devonian and Carboniferous. Of *Haplostigma irregulare* from the Devonian of South Africa, first described as a species of *Bothrodendron,* Seward remarks that in superficial characters it agrees more closely with *Cyclostigma,* a Devonian and Lower Carboniferous genus of lycopods, than with any other genus, but that it probably had a nearer relationship to the Psilophytales than to the Lycopodiales (60, *362*). Some of the branches of *H. irregulare* were bare, having few or no scars or appendages, but some of the stouter branches bore oval or circular scars, spirally arranged, without any sign of a leaf-cushion, ligule, vascular bundle, or parichnos. There is some evidence that these scars mark the insertion of spiny emergences and that the very narrow cylinder was either fluted or irregularly stellate in transverse section, features which recall *Asteroxylon.* It is interesting to compare this form with *Cyclodendron Mathieui* Sew. from what are probably Permian rocks of the Belgian Congo. Seward states that, while the systematic position of this fossil, of which no fertile parts are known, is not certain, there is a strong presumption in favor of including it among the Lycopodiales. The stems with their spirally disposed scars have a generally lepidodendroid appearance, though there are no leaf-cushions and apparently no ligules or parichnos. A single vascular strand seems to

have penetrated a little way into the very small scale-like leaves. Another feature strongly reminiscent of the Psilophytales is the very small size of the axial stele (1 mm.) and Seward notes that in its relatively small size as compared to the axis this strand agrees with the stele of a lepidodendroid branch. The proportions seem to be much the same as those found in some Psilophytales. It is not suggested that this late Palaeozoic fossil is a member of that ancient phylum, but merely that it has retained some primitive Psilophytalean characters and that it may show a phase in the vascularization of the emergence-leaf but little removed from that seen in *Asteroxylon.*

Thus, whether or not we regard the protuberances of *Rhynia Gwynne-Vaughani* as rudimentary prototypes of the spines of *Psilophyton,* we have a reasonably complete series of forms leading from the smooth axes of *Rhynia major* and other Psilophytales to forms with leaves like those of *Lycopodium.* It would seem natural to look upon the very small leaves of the Lower and Mid-Devonian *Protolepidodendron Scharyanum* and *P. wahnbachense* (38), in which both leaf and foliar bundle fork, as a further development of the emergence-leaf. As already mentioned, some botanists regard the leaves throughout the Lycopodiales as having originated during phylogeny as emergences. And it is certainly difficult to draw a line within the phylum dividing the leaves into two kinds. Among the Ligulatae, the leaves of some species of Selaginella are quite as small and, except for possessing a ligule, as simple as those of *Lycopodium;* and within the genus *Lepidodendron* are species in which the leaves are but a few centimeters long, while in others they reach nearly a meter in length, a size attained also by the leaves of some species of *Sigillaria* (*22, 182, 251*). In the latter genus, too, the foliar bundle was double, except in *S. Brardi* Brgnt., where it was single but had two strands of protoxylem. But, given the large size of the axes of these plants, there is no reason for supposing that their leaves would not increase in size, even if originally emergences, or their foliar bundle fork. And *Sigillaria* is a geologically younger genus than *Bothrodendron* and *Lepidodendron* in which the bundle is single. Nevertheless, it would be rash to assert that all lycopod leaves have been derived from emergences, nor is it easy on such a theory to account for the ligule, its early

appearance and its constancy in certain groups. Is it an emergence from an emergence? Since we know that parallel development has been extraordinarily prevalent during evolution, it is by no means unlikely that, besides the series of emergences rising throughout the ages to the status of microphylls, there may have been in the Lycopodiales other series of forms in which simple, *i.e.,* unbranched, thalloid branches of a relatively high order became, as Tansley once suggested (62), converted into comparatively large and simple leaves. Such branches might well have possessed an emergence, retained during their evolution into leaves, which eventually became fixed in position and constituted the ligule. If this was so in *Selaginella* its leaves have undergone considerable reduction. Two doubtful but interesting fossils lend some support to this view. One, a nameless fossil of great antiquity from the Yeringian (Upper Silurian) rocks of Victoria (45)[6] seems to have had a stem usually over 1 cm. across and bearing long, narrow, simple, crowded leaves, about 2 cm. long and 1 cm. wide. In some cases they show a median line, probably representing a vascular bundle. Seward says of these remains that they differ "in appearance from any previously recorded plant" (61). They do, however, somewhat resemble a form from the Upper Devonian of Gilboa, New York, which Goldring described as *? Sigillaria gilboensis,* while admitting that it was doubtfully a *Sigillaria* at all (17). The Upper Devonian plant is on a larger scale than the Yeringian one. Its leaves, when mature, sometimes exceeded 27 mm. in length, but in general proportions the plants are not unlike and the long simple leaves are a striking point of similarity. In neither case do we know anything of the fructification. Lang and Cookson, who described the Yeringian fossil, pertinently remark that, though it is natural to think first of the Lycopodiales, the probability must be borne in mind that some primitive plants had their lateral branches differentiated as long and simple leaves. If some of the larger adventitious branches, not infrequently found at the insertion of the hemispherical protuberances of *Rhynia Gwynee-Vaughani* were to become flattened, we should get leaves of this type. The branch need not, of course, have been adventi-

[6] The age of these rocks, left doubtful in 1927, has since been confirmed (46).

tious, but such branches might well be unbranched and simple at origin and thus a step nearer to a simple leaf.[7]

If we widen our conception of the Lycopodiales and include *Barrandeina* and *Duisbergia* among them, or if we look upon these two genera as closely related to the primitive Lycopodiales, we should probably be inclined to take Zimmermann's view that the leaf of lycopods has undergone reduction. But there seems little ground for believing that these plants were lycopods. In *Barrandeina* (36, 40, 14) the decurrent bases of the leaves give the stem a superficially lepidodendroid appearance, but the leaves themselves were several times forked and showed parallel (or dichotomous) venation. In association with numerous German and one Norwegian specimen of *B. pinnata,* there were found fragments of a *Psygmophyllum* leaf. It seems likely, from the form of what remains of the leaves on the stem of both species of *Barrandeina, B. Dusliana* and *B. pinnata,* that some of the oldest leaves among those referred to the provisional genus *Psygmophyllum,* which clearly includes remains of more than one type of plant, belong to *Barrandeina* or allied plants. The identification of fertile parts of *B. Dusliana* supports the lycopod affinity, for it has been shown that numerous oval sporangia are associated with each leaf. Owing to poor preservation, the mode of insertion of the sporangia could not be determined. While they did not appear to be inserted directly in the axil of the leaf, it could not be ascertained if a "sporangiophore" arising from the axis was present or if, as seemed to be the case in one or two places, a repeatedly forked structure was sterile distally and fertile proximally (40, *22*). *Duisbergia,* too, hardly seems to be

[7] Since the above paragraph was written Lang and Cookson have published a fuller account, founded on further specimens, some of them of undoubted Mid-Silurian age, of the plant from the Yeringian rocks and have named it *Baragwanathia longifolia* (Phil. Trans. Roy. Soc. Series B. **224**: 421. 1935). Some of the leaves of the new specimens reached a length of 4 cm., a size which does not materially diminish the gap in size between its leaves and those of the Gilboa fossil, since these latter sometimes exceeded 27 cm. *Baragwanathia* had a dichotomously branched axis and, in certain regions of the stem, reniform homosporous sporangia about 2 mm. in width and length were associated with and probably borne on the upper surface of spirally inserted leaves. The axial xylem was stellate in outline and without definite protoxylem or, so far as known, secondary elements. The xylem of axis and leaf consisted entirely of annular tracheids. The disposition of the sporangia strengthens the affinity with the Lycopods. As Lang and Cookson point out, *Baragwanathia* gives no support to the view that simple leaves were derived from emergences.

a lycopodial type, for the large and spirally inserted leaves with decurrent bases had numerous, apparently parallel but probably dichotomous veins. At the base of the lamina is a protuberance (a ligule?), while between some of the leaves are found cylindrical structures about 2–3 cm. long, believed to be sporangiophores. In the best preserved specimens Kräusel and Weyland thought that towards the proximal ends of these they recognized two depressions, believed to be caused by two laterally inserted, swollen and more or less circular bodies. The axial stele consisted of very numerous, long, irregular bands of xylem, surrounded by a zone of radially disposed ("radial verlaufende") bands, associated in pairs (presumably leaf-traces). Kräusel and Weyland compare the stele to that of *Cladoxylon,* with which, as they point out, *Duisbergia* seems to have no real affinity, and to that of certain species of *Lycopodium* (36). Though the banded stele is reminiscent of similar steles of some species of *Lycopodium,* the leaves and double leaf-trace are very different. As we know of many cases of parallel stelar development, we can hardly regard the central cylinder with bands of xylem as an important indication of affinity. The presence of a ligule, if this should be established, would be a more definitely lycopodial feature, but, as Kräusel and Weyland are careful to point out, it is not proved that the protuberance of *Duisbergia* was of this nature. Moreover, *Duisbergia* shows no resemblance to any known ligulate lycopod. If the club-shaped bodies are sporangiophores, the fructification is by no means lycopodial, unless Bassler's view that his *Gantheliophorus* was a sporangiophoric lepidophyte be accepted (3). This point lies outside the scope of the present essay and it can merely be pointed out that such a view is not generally accepted (4). Hirmer (*22, 285*) does not even mention *Gantheliophorus* and refers to it under the heading of literature dealing with *Mazocarpon.*

Kräusel in 1932 pointed out that it was doubtful if *Barrandeina* and *Duisbergia* represented a side branch of the Microphyllineae or a special group of the Macrophyllineae (33), and in a later paper he and Weyland leave it an open question whether *Duisbergia* should be associated with the lycopod or be placed in a separate group with *Barrandeina.* They even indicate, in passing, that if Nemejc's proposal to establish a new pseudomacrophyl-

lous group, the Noeggerathiales (50), should prove justified, *Barrandeina* might perhaps be brought into relation with *Noeggerathia*.[8] Until we know more of *Duisbergia* and *Barrandeina*, particularly of their fructifications, we can not, as Kräusel and Weyland truly remark, use them as a foundation for phylogenetic speculations, but on the present scanty evidence *Barrandeina* appears less remote from the Noeggerathiales than from the Lycopodiales.

THE FORERUNNERS OF MEGAPHYLLOUS PLANTS

Before the discovery of the *Rhynia* plants, Halle drew attention to the absence in the Lower and Middle Devonian of laminae even on well preserved fossils which showed most of the characteristics of fern fronds. He suggested, though with much caution, that the fern-like laminated frond of later geological horizons might be derived from a type such as that which he described as *Psilophyton Goldschmidtii*,[9] in which some of the lateral thalloid branches appear to have acquired slight dorsiventral symmetry and perhaps limited growth (19, *38*). Seward, in commenting sympathetically on this suggestion, remarks that the development of a frond from bare lateral branch-systems is more clearly foreshadowed in the large, probably dendroid *Aneurophyton* (61, *122*). This genus, *Cephalopteris* (formerly *Cephalotheca*) and *Protopteridium* (including *Milleria* Lang) appear to form a natural group.[10] In *Aneurophyton* the large main axis bore lateral and highly compound sterile branch-systems, the branching taking place in more than one plane. Except for the ultimate ramifications, which were very small and narrow expansions devoid of vascular tissue, there was no laminar development. The sporangia were borne on smaller separate branch-systems on which only an occasional sterile leaflet was present.[11] In the Upper

[8] For the affinities of the Noeggerathiales, see reference 8.

[9] As we are dealing with the mode of origin of the laminated frond and not discussing what genera gave rise to the earliest ferns having fronds, the fact that the remains united under *Ps. Goldschmidtii* are probably of doubtful specific value (44) or possibly belonged to various plants (26, *362*) does not invalidate this suggestion. For the difference between such a phylogeny of characters (the "Merkmalphylogenie" of German authors) and ordinary phylogeny, see Zimmermann (63, *11*) and Kräusel and Weyland (36, *352*).

[10] *Eospermatopteris* Goldring (16, 17, 18) may have been a seed-bearing relative.

[11] For fuller accounts of *Aneurophyton* see Aderca (1) and Kräusel and Weyland (34, 35, 36).

Devonian *Cephalopteris mirabilis* Nath. the axis bearing the large branch-systems has not been recognized. Each secondary rachis at once gave off catadromically a short fertile branch which by rapid and repeated dichotomies gave rise to a mop-like cluster of very numerous sporangia. This first branching of the secondary rachis may probably be interpreted as an unequal dichotomy, the stronger shank forming the prolongation of the rachis. This view is supported by the fact that the next pinna borne on the latter was also catadromic, though thereafter the pinnae are alternately anadromic and catadromic. The secondary rachises are united in pairs, alternately on the back and front sides of the primary one, suggesting that the foliar bundle may have been of the tetrapolar type of the Dineuroideae (*22, 516, f. 623, 624*).

Of Protopteridium, four Mid-Devonian species have been recognized: *P. hostimense* Krejci, *P. Piedboeufi* Kräusel and Weyland (not yet described), and two species from Scotland, *P.* (*Ptilophyton*) *Thomsoni* Dawson (*Milleria Thomsoni* Lang) and *P.* (*Milleria*) *pinnatum* Lang. The Scotch fossils are represented by branch-systems, fertile in their upper part where a number of short lateral branches bear, probably after subdivision, terminal sporangia about 4 mm. long and under 0.5 mm. wide. The connection of these parts has been observed only in *P. Thomsoni.* The lower sterile branches are several times divided. In *P. pinnatum* the ultimate divisions are slightly flattened and widened, this being the only laminar development observed (41, 42).[12] *P. hostimense* consists of large and highly compound branch-systems, ramifications of the sixth order having been observed. Their construction is fundamentally sympodial and pinnate, but traces of dichotomous branchings remain (for further details see Kräusel and Weyland [40]). All the branches are cylindrical without any laminar expansion and contain a vascular strand. The elongate sporangia, 0.5–0.6 mm. wide and 3–4 mm. long, are borne terminally on filiform dichotomous branches. Kräusel and Weyland leave it an open question whether these branch-systems represent the main body of the plant or the branched rachises of a naked but otherwise frond-like appendage of an axis. In both *P. Thomsoni* and *P. pinnatum* the branchings seem to have been in one plane and this suggests that we are

[12] In *P. Thomsoni* the distal ends of the lower branches are not preserved.

dealing with a laterally borne dorsiventral member, that is, a compound frond, presumably borne on an axis (42).[13] Kräusel and Weyland say that the strand of *P. hostimense* at once reminds one of *Lyginopteris* and even more of the Lower Carboniferous stems (*sic*) of unknown attribution described as *Lyginorachis* (40, *8*). The bundles which resemble those of *Protopteridium hostimense* are of course those of *Lyginorachis,* a genus founded for isolated petioles resembling those of *Lyginopteris,* and those of the petioles of *Lyginopteris.* The similarity, as they point out, is especially close with the vascular bundles of some recently described species of *Lyginorachis* (13, *pl. II, f. 3*) and this strengthens the view that the branch-systems of *P. hostimense* were appendages of an axis.

There seems to be some evidence that the Scotch species of *Protopteridium* were cryptogams and perhaps heterosporous. From the three localities in Scotland whence Lang got his specimens of *P. pinnatum* he obtained "multitudes of spores of a number of distinct types" (41, *255*). Now seeds would be at least as likely to be preserved as these spores, but not a single example has been recorded. The evidence, though negative, is impressive from the number of spores preserved. As only about four other kinds of fossil plants have been recorded from these localities (41, *269*), it seems a fair presumption that some of these spores belonged to *P. pinnatum,* though at the time, however, Lang was not able to draw even tentative conclusions about the groups of plants to which the eight different types of spores described by him belonged (41). Later he found an isolated spore attached to the wall of the sporangium of *P. Thomsoni* of the type previously described by him as type B (42). This is a somewhat specialized type of spore with a finely granulated wing; it is said to be common in the three localities from which *P. pinnatum* comes. There is thus at least a suggestion that this type of spore may belong to the latter plant. The spore is found in two sizes; in the larger the diameter is 200μ including the wing and 175μ excluding it, while in the smaller one, to which the spore in the sporangium of *P. Thomsoni* belonged, the corresponding measurements are 140–150μ and 100μ respectively.

[13] Kidston suggested that a large stem described as *Caulopteris Peachi* and found in the same locality as one of the specimens of *P. Thomsoni* might be the axis of this plant (*42, 789*).

The existence of two sizes in spores of similar type might as well indicate that the spores in question belonged to a heterosporous plant showing a definite but early stage of heterospory as that related species were concerned. That heterospory was in process of evolution in the Middle or Lower Devonian seems by no means unlikely. Lang notes that many of the spores from these formations are remarkably large for pteridophytic homospores or pteridospermous microspores, though smaller than any of the megaspores known from the Upper Devonian or Carboniferous, or even than the megaspores of existing plants (44, *269*). The largest type of spore described by Lang from the Cromarty beds in his type F, ranging from 250μ to over 400μ in diameter. It is said to be of general occurrence in all three localities but not usually abundant, a point which gives some slight support to the theory that it is a megaspore, since these are produced in smaller numbers than microspores or homospores. It is presumably of this type that Lang thought when he wrote that only the very largest of the Cromarty spores approached the size characteristic of megaspores. In cases of incipent heterospory the difference in size between the spores would naturally not be great. In *Noeggerathia foliosa* megasporangia and microsporangia were externally indistinguishable (49) and this seems to have been true also of *Calamostachys Casheana* Will. (52, frontispiece; 22, *403, f. 487*), where the megaspores were only 180μ and the microspores 40μ in diameter.

While it is generally admitted that the question is an open one, there seems to be a tendency to place *Aneurophyton,* at least provisionally, among probable pteridosperms. Kräusel and Weyland hold that there is no proof that this form was a pteridosperm, though there are some things in favor and nothing against such a view (35, *132*). Seward places *Aneurophyton, Protopteridium* (as *Milleria*) and *Cephalopteris* among probable pteridosperms (58, *537;* 61, *147, 153*). Hirmer places *Cephalopteris* after the Zygopterideae and *Protopteridium* (as *Milleria*) among ferns, *sensu lato,* that are insufficiently known. The exclusion of *Aneurophyton* from the first volume of his textbook (the only volume yet published) seems to show that he looks upon this plant as probably a pteridosperm (22). The similarity between *Aneurophyton* and *Eospermatopteris* has undoubtedly contributed

to this tendency. The evidence is strongly in favor of *Eospermatopteris* being a seed-bearing plant, but, as Kräusel and Weyland remark, this is not definitely proved. As Zimmermann pertinently remarks, it might be a form showing marked heterospory (35, *132;* 63, *251;* 16; 17; 18). And, admitting that it was a seed-plant, that would not prove that all members of the group to which it belonged had evolved seeds.

Kräusel and Weyland's comparison of *Aneurophyton* to the Upper Devonian *Palaeopitys Milleri* and to the Lower Carboniferous *Stenomyelon,* especially to *S. tripartitum,* does not help us much as to its affinity. We know so little about *P. Milleri* that, as the last authors to describe it point out, it is not even certain if it was a pteridophyte or a gymnosperm (32, *416*), though the xylem was of a typically gymnospermous type. Apart from the presence of a triarch or possibly exarch protostele in one very small specimen of *Stenomyelon tripartitum* (the larger specimens show three strands embedded in parenchyma), not a character necessarily indicating affinity, the chief similarities between the latter plant and *Aneurophyton* are the structure of its secondary wood and the absence of leaf-traces in the three fragments. These features, so far, are all that is known of it. But if, as has been suggested (53, *142*), this latter character is due to the length of the internodes, then the apparent similarity is deceptive; while, if there really were no leaf-scars in *S. tripartitum,* then the species must be removed from *Stenomyelon.*

Admittedly, the anatomy of *Aneurophyton* and *Protopteridium* is more pteridosperm-like than filicinean.[14] It must be admitted that, as Scott remarked, the sporangia of *Protopteridium* are quite unlike anything known in the true ferns (56, *365*). Such elongate and terminally borne sporangia seem to be more easily compared to those of the Rhyniaceae than to any other known sporangia. It is in the combination of advanced pteridosperm-like anatomy with a primitive form of sporangium and a relatively primitive morphology of the shoot that the interest of *Protopteridium* lies. May we not have in the latter a member of the group of thalloid vascular plants from which both the frond-bearing

[14] Well developed secondary wood was, however, characteristic of the Palaeozoic coenopteridacean *Botrychioxylon paradoxum* Scott (52, *319*) and of *Zygopteris primaria* Cotta (57). Some secondary xylem occurs also in modern *Botrychium.*

groups, ferns and pteridosperms, took their origin? If it should be so, *Protopteridum* is a relatively advanced member of the group, not itself a common ancestor of ferns and pteridosperms. But in the form of the sporangia and in the absence of differentiation of the lateral branches, complex though they seem to have been in *P. hostimense* at least, as leaves, *Protopteridium* has retained characters, believed to be primitive, that have not yet been found associated in any fern or pteridosperm known to us.

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Explanatory Notes

The geological periods mentioned, beginning with the most ancient, are the Silurian, Devonian, Carboniferous, and Permian. A land flora is generally considered to have first appeared in the Devonian. Even at the end of the Permian true flowering plants had not developed.

anadromous: having the lowest secondary branches originating on the anterior (upper) side of a pinna (Webster).

catadromous: opposed to anadromous, and having the lowest inferior segment of a pinna nearer the rachis than the lowest superior one (Webster).

columella: the axis of the capsule (sporangium) in bryophytes.

dichotomy: a system of branching produced by repeated forking of the growing point.

emergence: an outgrowth from the surface differing from hairs in arising from more than the superficial cells, and from spines in arising from a few layers only (Jackson).

exarch: having the protoxylem strands adjacent to the pericycle, toward the periphery of the stele.

Fibonacci symmetry: a symmetrical arrangement of parts in a system resembling the phyllotaxy of leaves.

heterospory: the possession of two different kinds of spores, distinguished by size or function or both, is characteristic of all seed-plants, of the water ferns, and the selaginellas.

homoplastic: having a similar structure or appearance not caused by phylogenetic origin from a common ancestor.

homospory: the possession of a single type of spore in the sporophytic generation, the homospore.

leaf-trace: the prolongation of the vascular system of the leaf into the stem.

ligule: a thin scale borne on the leaf above the sporangium in Selaginella and Isoetes. Plants with this structure are sometimes termed Ligulatae.

Lycopsida: Vascular plants have sometimes been divided into two groups, the Lycopsida and the Pterosida. The former, abundant in palaeozoic time but represented today only by the Lycopodiales and Equisetales, are characterized by small leaves (microphylls), sporangia on the upper or adaxial surface of the leaves, and the absence of leaf-gaps. The Pteropsida include all other Pteridophyta and seed-plants and are characterized by large leaves (megaphylls), sporangia on the lower surface of the leaves, and leaf-gaps.

paleae: chaffy scales found on many ferns.

parichnos: two strands of tissue near the center of the leaf-scar in *Lepidodendron* and *Sigillaria*.

lepidodendroid: resembling *Lepidodendron*, extinct plants of the Lycopodiales, with dichotomously branched, often large stems and narrow crowded leaves.

protostele: a solid stele, characteristic of most roots and of many pteridophytes.
protoxylem: the first xylem or wood formed in the development of a vascular strand.
Psilophytales: a group considered to be the most primitive vascular plants and to connect the algae with the pteridophytes.
pteridosperms: ancient plants combining the habit of ferns with the possession of true seeds. Many supposed ferns of the Carboniferous period are probably pteridosperms.
Pteropsida: see Lycopsida.
stele: the central cylinder of stems and roots, including the vascular tissues.
triarch: having three strands of protoxylem.
sympodial: branching by the development of lateral branches from a main axis.

CONTEMPORARY UNDERSTANDING OF BACTERIAL PLANT-DISEASES AND THEIR CAUSAL ORGANISMS

C. STAPP

Mikrobiologisch-chemische Abteilung der Biologischen Reichsanstalt für Land- und Forstwirtschaft, Berlin-Dahlem

At the turn of the century, the study of bacterial plant-diseases had already attracted much attention and provoked considerable discussion. Today it has acquired an impetus and a significance which warrant its recognition as an independent branch of science.

After it had once been indisputably established that certain plant diseases are definitely caused by bacteria alone, it is not surprising that many diseases whose causes had previously remained unknown were also regarded as bacterial in origin. A most heterogeneous array of bacteria were then described as alleged causal organisms. Many of these earlier claims, however, have since been proved erroneous. At that time, for instance, it was said to be definitely established that *Bacillus amylobacter* is the cause of damp-rot of potato and that *Micrococcus populi* is the causal organism of a disease affecting poplars in southern France. Passalacqua (78) described a leaf-disease of aloe in Palermo, attributing it to a spore-forming bacterium to which he gave the name *Bacterium aloes*. There was indeed *a priori* evidence for these early claims, since spore-forming bacteria were already definitely known in human diseases, such as tetanus and anthrax. It is well to regard all these early allegations with skepticism, since not one of the spore-forming bacteria, among which *B. amylobacter* is numbered, is conclusively known to be a true plant parasite.

The cocci likewise play no rôle in plant pathology, in contrast with their importance in human and animal pathology. The alleged pathogenicity of *Micrococcus populi* has not been proved (83, 84) and the claims of Brussoff concerning *Micrococcus ulmi* as causing death of elm trees have already been refuted (104, 109, 126). This lack of evidence is significant, notwithstanding claims to the contrary, as those of Lendner (61), who attributes death of elms in the streets, gardens and parks of Geneva primarily to *Micrococcus ulmi* and *Pseudomonas lignicola* and only secondarily to the fungus *Ceratostomella ulmi,* which is the real cause.

There is one group of bacteria, however, which have acquired importance among plant diseases, although relatively unimportant in human pathology. These are the fluorescent bacteria, so named because of their ability to produce a green fluorescent coloring matter. Many of them are known to be pathogens and to cause serious damage to plants; for example, *Pseudomonas tabaci,* the cause of wild-fire in tobacco, and *P. medicaginis* var. *phaseolicola,* the cause of halo-spot of beans. The great damage caused by these fluorescent bacteria[1] is primarily a result of their ability to gain entrance into uninjured plant tissues, in contrast with other bacteria which can enter a plant only through wounds or similar injuries.

The manifestations of these diseases and the action of their causal organisms may be quite varied. While typical wilt-diseases, for instance, are usually produced through the partial stoppage of the conducting tissue by great numbers of bacteria which frequently more or less completely clog the vascular bundles, in other diseases there is definite destruction of tissues. In the latter, chlorotic discoloration of the green parts frequently develops, or fluids appear in the intercellular spaces and the diseased areas assume a greasy water-soaked appearance. Increased oxydase activity sometimes ensues from disturbance in the balance of oxydizing and reducing processes in otherwise healthy cells, manifesting itself in dark discolorations. Black-leg of potato is such an effect caused by *Bacillus phytophthorus.* In damp-rot, on the other hand, there is dissolution of the middle lamella and union between cells is thereby destroyed, normal turgor of the cells decreases, cell-sap exudes, and a more or less viscous decayed mass results.

Not only destruction of cells is caused by these pathogenic bacteria, but they may also cause abnormal cell division and cell size in the host plant, as is evidenced by crown-gall of fruit trees and other plants as the result of invasion of *Pseudomonas tumefaciens.* In other cases, hypertrophy may first develop with subsequent

[1] The generic name *Phytomonas,* while customarily used in America for fluorescent bacteria which cause plant diseases, is deliberately avoided here, since a distinction based solely on a character so inconstant as pathogenicity is not sufficient. See also Stapp, Schizomycetes, in Sorauer's Handbuch der Pflanzenkrankheiten, ed. 5, **2**: 1–295. 1928, with mention of the older literature which, because of lack of space, can not be considered in detail here. For the same reason, authors' names are also omitted here after the names of host plants and species of bacteria.

destruction of the infected tissue. This is true of the pocket disease of sugar-beet caused by *Pseudomonas beticola,* of tuberculosis of olive caused by *P. savastonoi,* of canker, of oleander and ash caused by varieties of *P. savastonoi,* and of galls on *Gypsophila* caused by *P. gypsophyllae.* In this connection, mention may also be made of tumors on roots of *Coffea robusta* and *C. Klarinii* which Steyaert (116) attributes to *Bacterium coffeicola.*

Many species of the bacteria recognized as causing plant diseases are strictly limited to one host plant. Among these may be mentioned *Bacterium sepedonicum,* which can attack other plants after artificial inoculation but which in nature lives only on potato; *Pseudomonas stizolobii,* which grows only on *Stizolobium Deeringianum,* and *P. rubrilineans* which is confined to sugar-cane. Others are limited to a particular genus, as *P. translucens* on Hordeum, while still others can infect representatives of different and very remotely related families, such as *P. syringae, P. tumefaciens,* and *Bacillus amylovorus.*

It has usually been customary to bestow a new name on a disease and its bacterial cause if such a disease or any other with similar symptoms has not previously been known for the host concerned. In this manner many diseases and their causes have been enumerated during recent years, including the following:

Bacteriosis of pineapples (*Bacterium ananas*) in the Philippines (96).

Leaf-spot of *Ricinus* (*Pseudomonas ricini*) in Korea and Japan (47).

Spots on various organs of *Papaver Rhoeas* and *P. orientale* (*Bacterium papavericola*) (18).

On species of *Papaver,* including *P. somniferum* (*Bacillus papaveri*) (23).

Leaf-spot on species of *Viburnum* (*P. viburni*) (120).

Leaf-spot on *Berberis Thunbergii* (*P. berberidis*).

On *Carica papaya* (*B. papayae*) (82).

Damp-rot of sugar-beet (*B. betivorus*) in Korea (118).

Canker on plums (*P. mors-prunorum*) in England (127, 129).

Shoot-withering of plums (*P. prunicola* (128).

On rice (*P. itvano*) (122).

On *Holcus Sorghum* and *H. halepensis* (*P. holcicola*) (30).

On *Phaseolus vulgaris* (*P. phaseoli* var. *fuscans*) (20).

On *Cichorium Endivia* (*P. endiviae*) (56).
On *Salix alba* (*P. saliciperda*) (68).
On *Trifolium* and *Medicago* (*B. radiciperda*) (45).
On *Iris* (*P. iridicola*) (119).
On *Aleurites Fordii* (*P. aleuritidis*) (71).
On *Eugenia latifolia* (*P. hypertrophicans*) (99).
On pear (*P. utiformica*) (25).
On tomato (*B. punctulans*) (17).

In connection with previously unknown diseases of a plant, consideration has frequently not been given to the fact that a newly discovered pathogen may be the cause of a disease in one or more other species of plants. In other cases, the same disease has been attributed to different factors in different countries. Such has been the case with black-rot and damp-rot of potato, which in Holland has been attributed to *Bacillus atrosepticus,* in Germany to *B. phytophthorus,* in Canada to *B. solanisaprus,* and in Ireland to *B. melanogenes.* A still more striking illustration is a leaf-spot of tobacco, which was found in North Carolina, described as "wildfire," and attributed to *Pseudomonas tabaci*; another was described from Virginia as "angular leaf-spot" and connected with *P. angulata*; in Wisconsin the "Wisconsin leaf-spot" was associated with *P. mellea,* and finally in the Philippines an alleged fourth leaf-spot was attributed to *P. polycolor* (24). We shall later note that all four of these diseases are apparently identical.

Slight morphological, physiological, or cultural variations are not sufficient criteria for referring several diseases to different pathogens; neither can variations in the appearance of infected plants serve as the basis for such distinctions. Such variations indicate rather that every species of micro-organism possesses definite natural variability. It is known, for instance, that the same organism can form different colonies, some of rough, others of smooth appearance. Bryan (14, 15, 16) has observed in *Bacterium michiganense* not only the normal yellow but also a white or albino strain and a rose-colored race as well. Furthermore, she has likewise obtained white varieties of *Pseudomonas campestris, P. cucurbitae,* and *P. vesicatoria,* previously known only in yellow forms. Differences in virulence are associated with these variations in color.

There are, on the other hand, diseases which may be caused by different pathogens on one and the same host plant, such as damp-

rot on lettuce and endive. These damp-rots may be caused by any of the five bacteria *Pseudomonas viridilivida, P. vitians, P. marginalis, P. endiviae* (56), and *P. intybi* (112). These various bacteria are all distinctly different in physiological behavior and have only one character in common, that they all belong to the fluorescent group.

The number of species of bacteria described as entirely different from each other and causing plant diseases increases from year to year. Even the less critical plant pathologists may eventually wonder whether or not these innumerable species are legitimate. Fortunately, however, attempts have already been made to clarify the true status of these many species and such efforts may well deserve greater attention in the future. Comprehensive comparative studies of the species are necessary, involving serological tests in addition to the usual study of morphological, cultural and physiological characters. Not only agglutination reactions, but also precipitation reactions must be considered, since the former alone are insufficient while the latter are to be regarded as the most precise means of identification. When precipitation reactions are positive, identity of the species is unequivocally confirmed, even though there be definite cultural or physiological differences. If serological tests do not show complete identity, then we must group together those bacteria which closely resemble each other in producing similar pathological symptoms in the same host, and for the time being give them a single name, abandoning the others.[2]

Investigations of this nature have already been made on blackleg and damp-rot of potato, in which a total of 128 different races have been used, including the original cultures of *Bacillus phytophthorus, Bacillus melanogenes* and *Bacillus carotovorus*. Serologically these strains can be divided into five groups, the first one of which contains 111 of the 128 strains. In spite of the serological differences Stapp has proposed (101) the inclusion of all five divisions in one large group under the name *Bacillus phytophthorus*. He selected this name because the original strain of *B. phytophthorus* is one of the 111 races of the large first group, while *Bacillus carotovorus,* isolated and described from decaying carrots, matches a single other race, although its name has nomenclatural priority.

[2] Such a group is already known in medical bacteriology under the name *Bacillus coli* group.

Leach (59, 60), who has undertaken similar investigations, in part with the same pathogens, approves of this grouping but recognizes the priority of *B. carotovorus* and accordingly uses the name *B. carotovorus* group.

In a recent paper Stapp (107) describes a bacterium isolated from decayed hyacinths. It also belongs to the above-mentioned group, since it possesses features characteristic of the potato disease, but serologically it does not agree with the five sub-groups. This may be the same organism which Heinz first isolated in 1889 but described incompletely, to which he gave the name *Bacillus hyacinthi septicus.* Since this name is older than *B. carotovorus,* Leach must now refer to the group as the *B. hyacinthi septicus* group if he adheres to his principle of priority. That viewpoint would be justified if all the strains were completely identical, but since they are not, the name *B. phytophthorus* group may be retained, based on its most typical representative.

Link and Taliaferro (69) regarded the unlike agglutinization tests of the two damp-rot bacteria, *Bacillus carotovorus* and *B. aroideae,* as evidence that these two otherwise closely related organisms are distinct species. On the other hand, recent results of Orton and Stanley (77) indicate whither serological investigations may lead if proper technique is not or only incompletely observed. They seriously maintain that numerous damp-rot bacteria, such as *B. aroideae, B. carotovorus* and *B. phytophthorus,* and even certain leaf-spot pathogens such as *Pseudomonas tabaci,* a fluorescent bacterium, should no longer be regarded as distinct species but as variants of the *Bacillus coli* group.

As Stapp (100) has shown and Patel (79) confirmed, various strains of *Pseudomonas tumefaciens,* the organism of crown-gall, are not serologically identical, although they are all included in the one *P. tumefaciens group.*. Howard (40), on the contrary, found that strains of *Bacillus amylovorus,* the fire-blight organism, were serologically identical, even though secured from widely separated parts of North America and New Zealand. Williams and Glass (124) studied several strains of *Pseudomonas malvacearum,* the organism of the well known cotton bacteriosis and found them also serologically identical. According to Bryan (13), *Pseudomonas syringae,* the cause of lilac disease, is so similar to *P. citriputeale,* an organism causing black-pit of lemon, that they may be regarded

as identical. *Pseudomonas viridifaciens* and *P. vignae* may also be regarded as identical.

In 1930 Burkholder (19) made comparative studies of 18 species of *Phytomonas*; in 1932 Lacey (57) and in 1934 Clara (26) made similar studies of 15 and 19 species, respectively, of fluorescent bacteria. Additional comparative studies have been undertaken in recent years by others (36, 37, 75, 92, 98). All of these investigations have served to establish the identity of many so-called species of bacteria.

If Clara, who made comparative studies of two tobacco bacteria, had supplemented his physiological and infection experiments with serological tests, he would probably have been able to establish the identity of *Pseudomonas polycolor* and *P. angulata.* His suspicion that these bacteria represent one species was confirmed in 1930 when Stapp (103) showed that *P. angulata* and *P. tabaci* were serologically similar and consequently to be regarded as definitely identical.

The wild-fire bacterium of tobacco has attained significance in plant pathology because it is one of the few bacteria causing plant diseases in which toxin formation has been definitely established. This feature has long been known in organisms causing human diseases, such as diphtheria. As early as 1925 Johnson and Murwin called attention to the formation of toxin in *Pseudomonas tabaci,* but a detailed account was first given by Clayton (27) in 1934. According to him, *P. tabaci* forms toxin in all media in which it can develop. The toxin is thermostable, not precipitated by alcohol, neutral calcium acetate or lead acetate, and not destroyed by acids, but easily inactivated by dilute alkalies. When inoculated into leaves it destroys the chlorophyll, forming spots with chlorotic centers, typical of wild-fire. Such inoculations were successful on a whole series of plants, either with toxin alone or with toxin and bacteria together, and the reaction was stronger on many other plants than on tobacco. On these plants, in general, no infection was obtained by bacteria alone.

Development of technique for determining the resistance of tobacco to wild-fire is urgently needed, since the breeding of a resistant strain of tobacco is not only of scientific interest but of great economic importance as well. Stapp proposed a method in

1933 (108) which permits the inoculation of thousands of plants in a few hours.

A similar need obtains for determining the resistance of bush beans to halo-spot, *Pseudomonas medicaginis* var. *phaseolicola* (106). This disease, first discovered in North America in 1926, soon became very devastating and spread over whole continents. Numerous investigations have been made on the susceptibility of different kinds of bean (5, 21, 110, 111, 123, 130). There seems to be a few highly resistant varieties of bean in the trade and many which are very susceptible.

Jones (46) has published a method for determining resistance of alfalfa to the bacterial wilt caused by *Bacterium insidiosum.*

There is one bacterial disease, already mentioned several times, which for years has attracted unabated attention. This is the crown gall, found in all fruit-growing countries and caused by *Pseudomonas tumefaciens.* The patriarch of plant-bacteriology, Erwin F. Smith, devoted a good share of his life-work to the study of this disease and its cause. It is of much interest that this tumor, bearing many resemblances to those of animals and man, is caused by a definitely known bacterium, while a similar organism has occasionally been found in sarcoma and carcinoma but has not been considered as their cause. Though the causes of human cancer are admittedly various, they are not of a parasitic nature, even though a few irreconcilables have not yet forsaken the search for a causal organism. The alleged experimental proof that *Pseudomonas tumefaciens* is filterable, possessing a more or less invisible stage in its development, has also been discredited, together with the associated assumption of Lieske (66, 67) that this filterable phase might be responsible for human tumors (12, 49, 93, 95, 114). Similarly, definite proof of filterable phases of the bacilli of diphtheria, tuberculosis and typhoid has not been secured, in spite of numerous claims. Neither is it justified to draw general conclusions concerning the development and treatment of human tumors, as Lakhovsky has done (58), from apparently successful treatment of plant cankers. Lakhovsky claims to effect complete healing of tumor-bearing geraniums by binding them with coiled springs of copper wire of a particular diameter. Subsequent trials by Stapp and Bortels (115) have shown the complete futility of the claim.[3]

Schmidt (95) has also reported negative results in similar experiments.

Rivera (91) grew plants of geranium inoculated with *Pseudomonas tumefaciens* in chambers from which atmospheric rays, especially cosmic rays, were excluded to various degrees. In lead chambers cancerous growth developed rapidly and usually bore aerial roots, while in wooden compartments tumor-formation was slow. He concluded accordingly that certain rays which penetrated the wood, perhaps cathode rays, retarded cell division and conjectured that ionization of the air was also concerned.

According to Klein and his colleagues (51, 52, 53) the respiratory and metabolic activities of tumors are quite different from those of healthy tissues. In all plants there is a greater abundance of albumen in infected areas. The quantity of soluble inorganic and organic nitrogenous compounds as ammonia, amino-acids and amides differs in cancerous and healthy tissues, as well as the content of ash and acid. Catalase and peroxydase activities are also greater in the tissues of tumors.

Milovidov (72) was able to demonstrate an abundant development of typical plastids and of tannin in cancerous cells. On the basis of pH determination in tumors, Berridge (4) supposes that tumor-formation is associated with healing-reactions similar to those of wound-tissues.

Schimmel (94) has shown that the sugar content in hypertrophied tissues of the sugar-beet, tumors of which may become considerably heavier than the beets themselves, is generally less than in healthy parts of the same beet. Invert sugar, however, is always more abundant in the tumors. Since the ash-content may also be sometimes two or three times as great as in the normal tissues, Schimmel says there can be no doubt that the tumors draw food-stuffs from the beets.

Stapp and Bortels (113) have shown that development and form of tumors are largely dependent on the constitution of the host plant. Vegetative growth accelerates the formation of tumors, while flowering and fruiting exert an inhibiting effect. If vegetative growth of geranium, tomato or Datura is prolonged by early

[3] In a letter to the author dated March 5, 1934, Lakhovsky claims that slight inclination of the ends of the spiral toward the earth and orientation of its opening toward the north are necessary for success. Only negative results have been obtained in checking this procedure.

removal of developing flower buds, tumor development is favored; if the inception of the reproductive period is hastened, the contrary effect is secured.

There is still considerable discussion (62, 63, 76, 125) whether cancer-cells contain one or more nuclei or have an abnormal number of chromosomes. When Kostoff and Kendall (54, 55) inoculated tomatoes and later severed the stem above the tumor, sprouts occasionally developed from the tumors. If these sprouts, with part of the stem and tumor, were planted in earth, the roots which developed from them about 3 cm. above the tumor were all tetraploid; they possessed 48 chromosomes, while the original plants had only 24. In certain parts of the sugar-beet cells were found with 36 and even 72 chromosomes, while the normal number is only 18. Such tetraploidy is not regarded as the cause of tumor formation, although it may be an important factor in the development of new species. Tumors may develop upon the aerial parts of a plant as well as upon the subterranean organs. Barrett (1) has reported a genuine case of aerial crown-gall on the Golden Ophelia variety of greenhouse rose, among more than 3,000 plants of which not one was uninfected.

Recent investigations have also dealt with the biology of the crown-gall organism. Kauffman (50), Israilsky (42) and Israilsky and Starygin (43) have discovered two growth forms of *Pseudomonas tumefaciens,* the rough and the smooth, which frequently appear in cultures. Israilsky (42) claims to have isolated this organism or a very similar one from the tubercles of lupines; even the fixation of nitrogen is attributed to them. Such surprising discoveries must however be accepted with reserve.

Stapp and Bortels (114) have observed in living preparations the formation and disintegration of the so-called bacterial stars. These result from the assembling of separate motile rod-cells with protoplasmic connections. Star formation is distinctly favored by the addition of iron and manganese to the nutrient medium, by an abundant supply of oxygen, and by a high ratio of carbon to nitrogen in media with a relatively low supply of foodstuffs. After plasmic coalescence the disintegration of the star takes place and the protoplasm loses the viscous thread-producing nature which it had during the formation of the star. The individual cells again begin to divide and the young cells to swarm. The significance of

star formation is still undecided. There is at present no proof that it is a sexual process and the claim that it is such is very premature.

Rivera (90) claims that the crown-gall organism is injured by radium. He assumes that the gamma rays inhibit its growth while the beta rays cause its death.

It has long been known that *P. tumefaciens* can enter a host plant only through wounds and afterwards form tumors (80), but some supplementary experiments by Schmidt (95) may be mentioned. Schmidt germinated sterilized sunflower seeds on agar plates carrying a culture of the crown-gall organism. After 10 to 22 days the seedlings were transplanted into pots in soil; in no case did tumors appear on the plants. Fresh cultures of *P. tumefaciens* were smeared on pieces of rubber and tied to plants 10 to 25 cm. high with uninjured epidermis; the results were all negative. Plants were then placed in a partial vacuum and covered with an aqueous suspension of the bacteria. After re-admission of the air, the liquid penetrated the stomata and partially filled the intercellular spaces; on further growth of the plants the results were still negative, while in slightly injured plants tumors developed in every case after similar treatment. Banfield reports (2) the occasional presence of the bacteria in quantity on the surface of the tumors and has also found them in water in which tumors had been lying a short time.

There have also been recent investigations on the rate of transmission of *P. tumefaciens* within plant tissues. Hill (39) observed penetration in young tomato stems at the rate of 0.04 mm. per minute for the first quarter-hour and 0.03 mm. per minute for three hours thereafter. Since Ivanoff and Riker found the rate of diffusion of dead bacteria and of india ink to be the same, they conclude that the spread of the organism in tissues depends primarily on purely physical forces such as capillarity and negative pressure.

Bacteriophage has heretofore played no part in phytopathology. We may well give consideration to the interesting investigations of Chester (22), supplementing previous research on bacteriophage in the crown-gall (12, 73). He sought for bacteriophage both in and on the host plant and found it in healthy tissue adjoining the crown-gall in stems of geranium, but not in healthy uninfected plants. In the beet he found it in healthy uninfected plants.

From this he concludes that bacteriophage can diffuse from the point of infection into healthy tissues and that it can penetrate into healthy sugar beets directly from the soil, where it must be present. Chester also produced crown-galls by using strains of *P. tumefaciens* completely free from bacteriophage and thereby contradicted the claim of D'Herelle and Payre (28) that tumors are provoked by this organism only in connection with an invisible form. Gäumann (34) supposes that bacteriophage is not formed by destruction of the bacteria, but that its development is connected with a living reaction of the infected tissue. He concludes there must in some way be concealed here an immunizing reaction, a production of anti-bodies.

According to Thung (121) the crown-gall organism does not form toxin in bouillon cultures. He agrees with Magrou (70) in believing that its ability to form tumors may be attributed to the action of mitogenetic rays.

The number of plant families which are known to include hosts for the crown-gall has also increased. Muncie (74), for example, found crown-gall tumors on the roots of dock, *Rumex crispus,* in a raspberry field in Minnesota and on the rhizomes of rhubarb, *Rheum raponticum,* in a nursery in Iowa. Crown-gall has also been found on cypress, *Cupressus arizonica,* by Brown (6), on willow, *Salix caprea,* by Rainio (81), on cedar, *Juniperus Sabina,* by Brown and Evans (11), and supposedly on elm by Emery (32).

Levine (64, 65) succeeded in producing tumors on the giant cactus, *Carnegiea gigantea,* and on prickly pears, *Opuntia,* sp., by artificial inoculation. As early as 1926 Stapp successfully inoculated *Opuntia* (results not yet published), resulting in a tumor the size of a fist. This plant, now nine years old, has heretofore appeared to be alive, but since 1933 has lost all its cladodes above the tumor.

Since the first basic investigations of E. F. Smith and his colleagues on crown-gall in 1911, it has been assumed that the deformity of apple trees known as hairy-root is also caused by *Pseudomonas tumefaciens.* In 1929 and 1930 Riker and his colleagues gave proof that hairy root is caused by *P. rhizogenes,* a species closely related to *P. tumefaciens* but not identical. Inoculation with *P. tumefaciens* produced only crown-gall; with *P. rhizogenes* only hairy-root was induced, and with mixed infections

both effects were secured. The results were the same whether the plants were grown in steam-sterilized soil or in untreated soil (87). Inoculations were also successful with a series of other plants, such as rose, sugar-beet, bean, and chrysanthemum, but only weak infections, if any, were secured on tomato or tobacco. Suit (117) isolated the same organism from *Spiraea Van Houttei* and *Spiraea prunifolia*. In 1934 Hildebrand confirmed Riker's results on the causal differences between hairy-root and crown-gall. According to him, *P. rhizogenes* is a typical wound-bacterium; he found it in large quantities on the outer surface of hairy-root tumors and frequently in the earth surrounding them. Within the tissues it was localized in the intercellular spaces. Hildebrand found great differences in the susceptibility of apples to this disease. He tested twenty-nine kinds in 1930 and noted variations from 12 to 100 per cent, and the following year found variations from 22 to 100 per cent in thirty-seven kinds. Previous infections did not prevent subsequent attacks. Harris (35) also found differential resistance among apple stocks, demonstrated both by the relative number of successful inoculations and by the size of the tumors.

Riker and Hildebrand (88) have shown that the incubation periods of hairy-root and crown-gall are relatively long in spring and autumn and shorter in summer. Temperature and active growth of the trees are apparently important factors. Root-infesting insects in the soil, such as Phyllophaga, Elateridae and Mycetophilidae, may play an important part in the spread of the diseases. Riker and others (89) have shown that hairy-root is apparently more abundant than crown-gall in nurseries in the United States, while in Germany it occurs to a very limited extent, if at all.

As a preventive measure Riker has advocated binding the young trees with tape at the contact between stock and scion. This method is scarcely applicable in Germany, where a different method of propagation is used, obviating the danger of infection at this point. On the other hand, Oppenheim's method of immersion in "Uspulun-Lehmbrei" has been found satisfactory and has been further recommended by Husz (41) in Hungary and by Boumann (4) in Holland. It is still undetermined whether treatment of the soil with chlor-picrin, with which Kapshuk (48) has experimented in Russia, will be of practical value.

In conclusion there may be mentioned the interesting investigations of Eglits (29) on temperature and respiration in healthy and decaying potatoes. He found that the heat of healthy potatoes is about 0.005° C. above the surrounding temperature. If the potato was wounded, there ensued within an hour a rise of temperature in the wounded tissues to about fourteen times the normal amount. This wound-temperature fell at first sharply and then slowly with the healing of the wound and reached normal in about two days. If the tubers were inoculated with *Bacillus phytophthorus,* the temperature rose with some fluctuations for 170 hours to 30 to 35 times the normal. At this temperature the tissue died and in consequence the temperature fell rapidly to subnormal. The curve of respiration rose similarly, reached its maximum 30 to 40 hours before the death of the tissue, and then fell rapidly. Thus there is a characteristic curve of increased temperature and respiration in diseased plant tissue, just as in the diseases of man, but the "fever-condition" in plants decreases with increasing distance from the seat of infection.

This short review, covering only a portion of the recent literature, may serve as introduction to a specialized field of botany which is of both scientific and economic importance.

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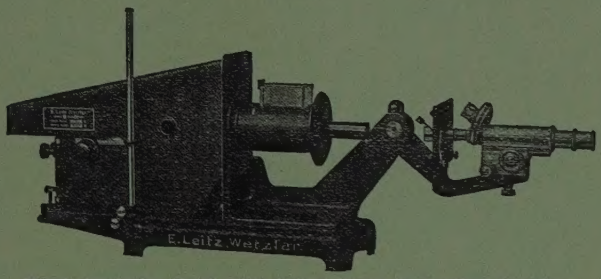

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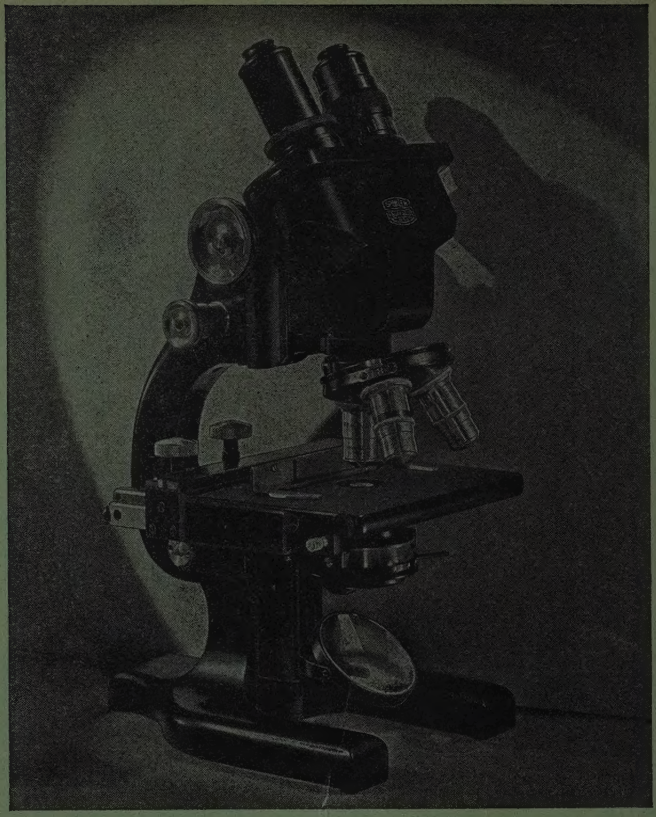

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